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Flight polymorphism observed in an alpine leaf beetle and associated costs

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ABSTRACT

Flight polymorphism in an alpine population of the leaf beetle *Oreina cacaliae* (Coleoptera: Chrysomelidae) was observed in the field. One part of this population engaged in flight in autumn and spring (flyers) whereas the other part did not fly and got active after overwintering, later in the season (nonflyers). The flyers fed on a spring host plant *Petasites paradoxus* Baumgartner since they emerged earlier than the main host *Adenostyles alliariae.* By comparing life history parameters of the two morphs of *O. cacaliae*, we tested possible costs associated with flight. Flyers (males and females) were smaller in size than nonflyers, measured as elytra length. Within the nonflyer group small females larviposited significantly fewer larvae than large females. Flying reduced reproduction and survival only when the beetles did not have access to food after their flights, which might represent the situation in the field since beetles risk not to be able to feed while flying from spring to summer host. Insect dispersal by flight may be an investment, by a portion of the population, in colonising and exploiting resources in new habitats, with a risk of reduced reproduction and survival.

KEY WORDS: dispersal by flight, cost, reproduction, survivorship, Coleoptera, Chrysomelidae, *Oreina cacaliae.*

INTRODUCTION

In several herbivorous insect species flight polymorphism has been observed. Advantages of the flying morph might be for the escape from deteriorating patches of host plants and for the colonisation of more nutritious and less crowded stands that occur elsewhere (Denno *et al.* 1989). But there may also be costs associated with dispersal such as increased predation risk or the failure to find a suitable habitat, as well as costs in terms of life history traits such as reproduction and survival (Roff 1984).

In many systems the difference in morphology between morphs is obvious without any tedious analysis of flight behavior, therefore wing polymorphism has provided an easy way to assess costs of flight. However, the costs assessed in such studies are often due to the possession of flight muscles and wings rather than to actual flight since winged individuals do not always migrate or even fly (Rankin and Burchsted 1992). In addition, flight activity is usually tested under artificial circumstances, the insect being fixed to a pin or tethered to a mill (Solbreck 1974).

In our *Oreina cacaliae* (Schrank) (Coleoptera: Chrysomelidae) system, we distinguish two classes of beetles: a) flyers, that leave their main host plant patch in autumn to overwinter away from their host plants and that emerge early in spring to fly to the spring host *Petasites paradoxus* (Asteraceae) where they feed until the main host *Adenostyles alliariae* Kerner (Asteraceae) comes out, and b) nonflyers, that overwinter in the ground below the host plant patches of *A. alliariae* and emerge in early summer at the same time as that host plant and never feed on another plant (Kalberer 2000).

The objective of this study was to determine whether there is a correlation between dispersal polymorphism and performance in *O. cacaliae* beetles. Specifically we examined whether flyers differed from nonflyers in: (1) fecundity, (2) size, and (3) survivorship.

METHODS

Beetles and Collection Sites

All beetles were collected in the Swiss Alps near La Fouly in the Val Ferret (Valais) at 1500 m above sea level (45°56'10" N latitude, 7°05'95" E longitude). The flyer group was collected on the spring host *P. paradoxus* and the nonflyer group was collected on *A. alliariae* as soon as this main host emerged. The flyers were collected between mid April (1998) and mid May (1997, 1999), and nonflyers between end of May (1997 and 1998) and beginning of June (1999). Beetles were sexed using sexual dimorphism of the tarsi (Lohse and Lucht 1994).

Male and Female Size

In 1998, the length of the elytra of 98 flyers and 144 nonflyers were measured with a calliper after collection in the field to determine whether there was a difference in size between the two groups. Data on size of male and female beetles in the flyer and nonflyer group, respectively, were analysed with a two-factor ANOVA using 'size' as the dependent variable and 'sex' and 'flying state' as factors.

Female Fecundity

The fecundity of female flyers and nonflyers was determined in the laboratory during the whole reproductive season for three consecutive years. Females were individually kept in plastic containers lined with a thin layer of moist plaster and a filter paper to ensure constant humidity. They were maintained in an incubator at a day temperature of 16°C and a night temperature of 12°C and a 16L: 8D regime. This ensured a temperature rhythm concordant with natural conditions in the field at the beginning of June. Every week, the number of offspring was counted, the occurrence of dead females was noted, food foliage and filter paper were replaced and the plaster bottom in the pots was moistened. The number of offspring was summed over the season, starting with the first day that a female larviposited. Observations were continued for at least three weeks after the last larva was found. In 1997, the females of the flyer group were fed with flowering *P. paradoxus* until the emergence of *A. alliariae*. As soon as *A. alliariae* from the field was available, both groups were fed with this main host plant, in all years. In 1998, the flyers were not fed in the four week period between their collection and the emergence of *A. alliariae* in the field. Because of the high mortality in the unfed flyer group of 1998, three groups were maintained in 1999: flyers not fed, flyers fed with *P. paradoxus* until the emergence of *A. alliariae* and nonflyers fed with *A. alliariae* from the beginning. Because nonflyers overwinter in close vicinity from the main host *A. alliariae*, it is very likely that they have access to food immediately after overwintering.

Female Survival

Every week we checked for female mortality in the plastic containers in the lab. A log-rank test was used to test for differences in survival curves between females of the unfed and fed flyers and nonflyers (Harrington and Flemming, 1982). A Bonferroni correction was used to adjust the critical significance levels for multiple pairwise comparisons (Rice, 1989).

Relationship between Number of Larvae Produced and Female Survival

To test the influence of survival time on reproduction, number of days living versus number of larvae produced in the flyer and nonflyer group of 1997 was subjected to a regression analysis.

RESULTS

There is no morphological difference detectable by eye to distinguish flyers from nonflyers in the field. By collecting flyers from *P. paradoxus* we were sure that they had reached that plant by flying in spring. The possibility that *O. cacaliae* overwintered in the soil or the leaf litter next to *P. paradoxus* and had not flown to these spring host patches after overwintering at sites away from *A. alliariae,* could be excluded, because in autumn beetles were observed at overwintering sites at a cliff away from both host plants and never close to *P. paradoxus*. In addition, the level of infestation of *P. paradoxus* patches seemed to be related to the distance from the nearest overwintering place with patches close to the overwintering place infested earlier than the ones further away. *O. cacaliae* beetles found on the spring host *P. paradoxus* at a distance between 75 and 450 m from their overwintering places were regarded as flyers, whereas beetles collected in a patch of *A. alliariae* at a time when this plant was producing its first leaves were considered as nonflyers. At the time the nonflyers were collected from *A. alliariae*, the flyers were still present on *P. paradoxus* flowers. Beetles were observed on *P. paradoxus* as long as this plant was flowering (flowering precedes leaf emergence in this species). Since we recaptured four beetles that had been marked the previous year in the same *A. alliariae* patch after one year, we can be sure that at least some beetles, nonflyers, stayed in the same host plant patch for at least two consecutive years.

Size of Flyers and Nonflyers

The size of the beetles (length of elytra) was measured in 1998. Male beetles, flyers as well as nonflyers, were smaller than female beetles of the same group (Fig. 1). Female as well as male flyers were smaller in size than nonflyers (two-factor ANOVA: MS=0.27, F=5.394, P<0.0211, n=54 female flyers, n=51 female nonflyers, n=44 male flyers, n=94 male nonflyers).

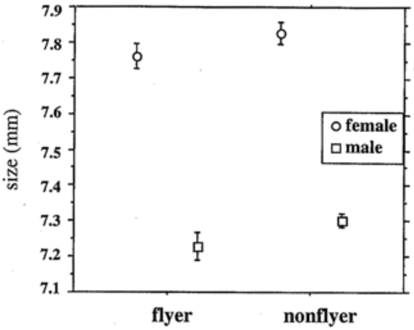

Fig. 1. Flyers (males and females) are smaller in size than nonflyers and males are smaller than females (mean size and SE, F= 5.4, P<0.02, for flying group, F= 313.8, P< 0.001 for sex, two factor ANOVA, n=54 female flyers, n=51 female nonflyer, n=44 male flyer, n=94 male nonflyer).

Larval Production

To analyze quantitative differences in the total number of larvae produced in the different flying group and the different years we used an ANOVA (MS=20682.7, *F*=30.56, *P*<0.0001, n=265) followed by a Bonferroni/Dunn post-hoc test. Unfed flyers produced significantly fewer larvae than nonflyers in 1998 and 1999 at the 5% level (Fig. 2). Interestingly, when flyers were fed (in 1997 and 1999), the total number of larvae they produced was not different from beetles of the nonflyer group.

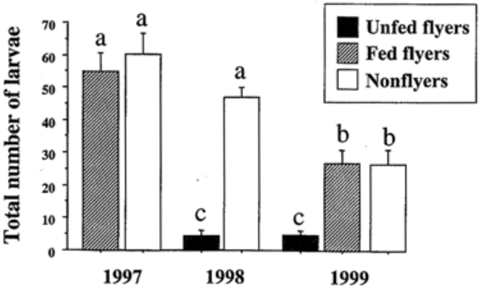

Fig. 2. Total number of larvae per female produced over a whole season in the different dispersal groups (mean and SE). n=39 flyer 1997, n=30 fed flyer 1999, n=50 flyer 1998, n=30 flyer 1999, n=39 nonflyer 1997, n=50 nonflyer 1998, n=30 nonflyer 1999. Different letters indicate significant differences (ANOVA: MS = 2082.7, F=30.86, P<0.001, n=265).

Female Survival

Female survivorship curves showed that less than 10% of the unfed flyers survived the first 28 days after larviposition had started, whereas between 55 and 90% of both, fed flyers and nonflyers lived longer than 28 days (Fig. 3). There was no difference in survivorship within the nonflyer group of the three years (log-rank test, Chisq=4.4, df =1, P= ns between 1997 and 1998; Chisq=0, df=1, P=ns between 1997 and 1999; Chisq=1.4, df =1, P=ns) and no difference within the unfed flyer groups (Chisq=0, df=1, P=0.86). Survivorship was significantly different between the unfed flyers and the fed flyers (Chisq=47.3, df=1, p<0.0001 for flyer unfed 1998/flyer fed 1999, Chisq=13.5, df=1, P<0.001 for flyer unfed 1998, flyer fed 1997, Chisq = 45.8, df = 1, P< 0.001 for flyer fed 1999 flyer unfed 1999, Chisq 15.2, df =1, P < 0.001 for flyer fed 1997/flyer unfed 1999).

Regression between Larva Production and Life Span

A positive relationship was found between female longevity and the total number of larvae produced (Fig. 4); ($y=11.34x+0.91$, R2=0.41, $F = 53.21$, $P<0.0001$, $n = 78$). The analysis was done with data from the flyer and nonflyer group of 1997, because in the flyer group of 1998 too few larvae were laid.

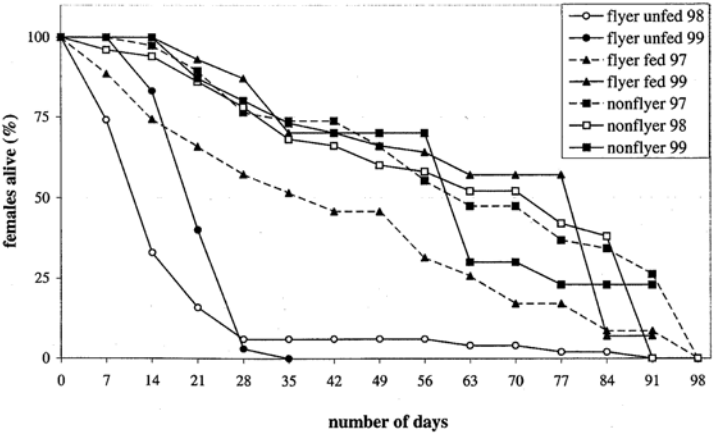

Fig. 3. Survival curves of adult *O. cacaliae* females of the unfed flyer (circles), fed flyers (triangles) and nonflyer (squares) groups during three years. Day zero is the day that beetles were collected in the field.

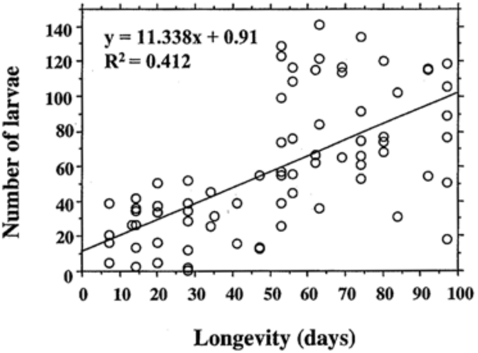

Fig. 4. Regression analysis on the number of larvae laid per individual female over the 1997 season (flyer and nonflyer) and the corresponding number of days that females lived ($F = 53.21$, P d$\leq$0.0001, n = 78).

DISCUSSION

The distinct flight behavior of *O. cacaliae* observed in Val Ferret allowed us to distinguish flyers from nonflyers. Like many other Coleoptera, males of *O. cacaliae* were smaller than females. The flyer beetles, males as well as females, were significantly smaller than the nonflyers. Sub-optimal nutrition in a bad host plant patch might have resulted in smaller beetles, thus it seems adaptive for small beetles to fly away from this environment and reproduce in another habitat. Roff (1991) suggested that bioenergetic constraints mandate that migrants should be as large as they can be to maximize the distance they can travel without refuelling, and thus predicts that migrants will be larger, on average, than nonmigrants. This prediction was not supported in *O. cacaliae*.

Preliminary observations suggested that wing size and beetle size are correlated, thus smaller beetles probably do not have a better flight potential in *O. cacaliae*. The *O. cacaliae* flyers produced significantly fewer larvae than the nonflyers, only if the flyers were not fed. Fed flyers produced as many larvae as nonflyers in *O. cacaliae*. Access to food before and after flight seems to be an important factor for the number of larvae produced. In other insect orders, access to food after flight was shown to be important to reduce the cost of flight on reproduction, too. In the migrant bug, *Oncopeltus fasciatus* (Dallas), flights of several hours over 6 days had no effect on life history characteristics of female bugs unless they were also starved over that period, which reduced fecundity and longevity (Slansky 1980).

Our mark-recapture studies with *O. cacaliae* showed that flyers travelled distances between 110 and 950 m when flying from spring to the summer host, and the risk not to be able to feed during that time is high since many beetles were observed on the snow away from any potential host. Therefore we consider that the situation presented in 1998, where the flyers were not fed in the lab, could be more realistic than the one of 1997 were the flyers were fed with *P. paradoxus* between their collection on *P. paradoxus* in the field and emergence of *A. alliariae*. The reality probably lies between these two extreme nutritional status.

As for reproduction, feeding after flight was an important factor for female longevity. For unfed flyers in 1998 and 1999 more than 90% of females died within 28 days after reproduction started, more than twice as many compared to fed flyer and nonflyer groups. In the unfed flyer group of 1998 and 1999, 60 and 85% respectively died within 3 weeks after collection, representing the approximate time they needed to find *A. alliariae* patches in the field (Kalberer 2000). The 1999 study, where a fed and an unfed flyer group were maintained together with a nonflyer group, confirmed that feeding is the factor leading to the difference in survival as well as in reproduction. Fed flyer beetles survived significantly better than unfed flyers in both years. Survival was linked positively with reproduction since the females continued to larviposit during three months.

O. cacaliae females do not need to remate in spring (Dobler and Rowell-Rahier 1996), but are able to start a new colony directly after overwintering. Nevertheless, mating in this species has been observed in spring, especially on the spring host of the flyers, *P. paradoxus*. Thus, if selection on males acts during the winter season, females may increase their fitness by remating with males that successfully overwintered (Stevens and Cauley 1989). In addition, sperm which became inviable during the winter may be replaced by remating in spring.

O. cacaliae lives in a relatively stable environment, where parasites are rare, in the Swiss Alps. *A. alliariae* patches provide everything beetles need to survive, reproduce and complete their life cycle. Those patches can persist for several years (some are known to us for more than 15 years). Nevertheless catastrophic events like flooding (as observed at a site in the Val Ferret in 1997 and 2000) can completely destroy a host plant patch within hours. In the absence of reliable environmental cues, it may be advantageous to spread the risk (den Boer 1968). Selection might have favoured individuals that produce heterogeneous offspring, some of which stay in the patch (nonflyers), and some of which disperse to other patches (flyers) (Davis 1984). Our results indicate that possible costs exist in survival and reproduction when the flying beetles have no access to food after flight. Since there is a high degree of patchiness in plant communities and beetles continually try to find high quality host plants, investing energy in dispersal may be justified.

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